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THE EFFECTS OF MORPHINE ON FIXED-INTERVAL PATTERNING AND TEMPORAL DISCRIMINATION

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Changes produced by drugs in response patterns under fixed-interval schedules of reinforcement have been interpreted to result from changes in temporal discrimination. To examine this possibility, this experiment determined the effects of morphine on the response patterning of 4 pigeons during a fixed-interval 1-min schedule of food delivery with interpolated temporal discrimination trials. Twenty of the 50 total intervals were interrupted by choice trials. Pecks to one key color produced food if the interval was interrupted after a short time (after 2 or 4.64 s). Pecks to another key color produced food if the interval was interrupted after a long time (after 24.99 or 58 s). Morphine (1.0 to 10.0 mg/kg) decreased the index of curvature (a measure of response patterning) during fixed intervals and accuracy during temporal discrimination trials. Accuracy was equally disrupted following short and long sample durations. Although morphine disrupted temporal discrimination in the context of a fixed-interval schedule, these effects are inconsistent with interpretations of the disruption of response patterning as a selective overestimation of elapsed time. The effects of morphine may be related to the effects of more conventional external stimuli on response patterning.

Key words: fixed-interval schedule, temporal discrimination, response patterning, timing, morphine, key peck, pigeons

Fixed-interval (FI) schedules of reinforcement have been widely used throughout the history of behavioral pharmacology and toxicology because the behavior maintained by these schedules is especially sensitive to alteration by drugs and other compounds (Branch & Gollub, 1974; Gentry, Weiss, & Laties, 1983; McAuley & Leslie, 1986). Fixed-interval schedules provide a reinforcer for the first response that occurs after a fixed time has elapsed and maintain a characteristic pattern of response: A pause follows the delivery of a reinforcer, after which response rates increase across the interval up to the delivery of the next reinforcer (Ferster & Skinner, 1957, pp. 133–134). Drugs from many pharmacological classes frequently increase low rates of response during the initial portion of the interval, but particularly with larger doses, they decrease higher rates during later portions of the interval (see, e.g., Dews & Wenger, 1977; Kelleher & Morse, 1968; McKearney, 1981; McKearney & Barrett, 1978; McKim, 1981; Sanger & Blackman, 1976).

Although the effects of drugs on behavior maintained by FI schedules are extensively documented, correspondingly little empirical attention has been devoted to understanding why these alterations occur (see Branch, 1984). Historically, drug effects on the temporal patterning of behavior maintained by FI schedules have been considered an example of rate dependency (Branch & Gollub, 1974; Maricq, Roberts, & Church, 1981; McAuley & Leslie, 1986; Sanger, 1987), which in its most basic form is the empirical generalization that the effect of a drug on behavior tends to be related to the rate of behavior in the absence of the drug (Dews, 1981). Specifically, with respect to behavior maintained by FI schedules, the effect of a drug on behavior tends to be inversely related to the rate of behavior in the absence of the drug.

Although rate dependency provides a general description of drug effects on behavior maintained by FI schedules, it does not provide a behavioral mechanism of drug action

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by which to understand these effects (Branch, 1984). The present experiment examined one possible behavioral mechanism: changes in discriminative control by time. Because the patterning of behavior maintained by FI schedules has been widely suggested to reflect temporal discrimination or ''timing'' (e.g., Catania, 1970, p. 6; Ferster & Skinner, 1957, p. 266; Keller & Schoenfeld, 1950, p. 86; Reynolds, 1975, p. 82; more recently, e.g., Church, 1997; Higa & Staddon, 1997; Killeen, Fetterman, & Bizo, 1997; Roberts, 1997), changes in patterning following drug administration may be interpreted to result from disruptions of that discrimination (e.g., Maricq et al., 1981; McAuley & Leslie, 1986; Meck, 1996).

Broadly, there have been two general suggestions regarding the disruption of temporal discrimination in the context of FI schedules. For example, Maricq et al. (1981) noted that the increase in response rate early in fixed intervals following drug administration is consistent with a general disruption of timing. Similarly, McAuley and Leslie (1986) maintained that increases in low rates early in fixed intervals are best described as changes in temporal control. By this interpretation, drugs change behavior maintained by FI schedules by changing temporal discrimination. A more specific temporal-discrimination explanation suggests that the effects of drugs on behavior maintained by FI schedules are not the result of a general loss of temporal control, but of a particular distortion in temporal perception. According to this explanation, drugs may increase low early rates because of an overestimation of elapsed time (e.g., Killeen, 1991; McAuley & Leslie, 1986) or an increase in the speed of a hypothesized internal clock (e.g., Maricq et al., 1981; Meck, 1996).

Although drug effects on FI performance have been interpreted to result from changes in temporal discrimination, changes in the patterning of behavior and changes in temporal discrimination may be difficult to isolate in typical FI schedule procedures. Catania (1970) distinguished between these aspects as two outcomes of temporally based schedules of reinforcement: differentiating effects and discriminative effects. Differentiating effects result ''when differential reinforcement acts on the temporal spacing or patterning of responses'' (p. 2). Discriminative effects result ''when the temporal spacing or patterning of events enters into the control of responding as a discriminative property of the environment'' (p. 2). Furthermore, Catania noted, ''the confounding of temporal discrimination with other temporal processes is inevitable when temporal properties of responding are involved in the measurement of discriminative control by temporal properties of stimuli'' (p. 12).

To conclude that changes in temporal discrimination occur at the same time that changes in response patterning occur on FI schedules, it would be useful to have a measure of temporal discrimination that is not inferred from response patterning. Discrimination of the passage of time may be directly assessed in FI schedules by interpolating temporal choice trials within intervals (Stubbs, Vautin, Reid, & Delehanty, 1978). In this procedure, pigeons' center-key pecks were reinforced on an FI schedule. Intermittently, the FI schedule was interrupted by the presentation of temporal choice trials. When a choice trial was arranged, the center key was extinguished independently of responding and the side keys were lit either a relatively short or long time after the beginning of the interval. Pecks to the right key produced food if the choice was presented after a short duration, and pecks to the left key produced food if the choice was presented after a long duration.

Using a similar procedure, the present experiment obtained independent assessments of the effects of morphine on pigeons' discrimination of the passage of time and response patterning in the context of an FI schedule. Morphine was chosen because in a recent direct assessment of its effects on temporal discrimination, morphine decreased accuracy only at a dose that decreased response rates (Wenger, McMillan, Moore, & Williamson, 1995). In that experiment, pigeons pecked the center key to initiate presentation of a short or long temporal sample. Pecks to a green side key produced food following short samples, and pecks to a red side key produced food following long samples. Accuracy of the temporal discrimination was decreased only at the dose of morphine that decreased response rates on the center key. Elsewhere (Odum, Haworth, & Schaal, 1998;

Odum & Schaal, 1999), morphine changed the temporal patterning of the FI performance of pigeons at doses that did not suppress overall response rates, suggesting that at moderate doses morphine could plausibly change FI patterning without changing temporal discrimination.

A further reason for choosing morphine is that its effects on behavior maintained by FI schedules have been shown to be rate dependent. Low baseline rates in the initial portion of the interval often increase and, particularly with larger doses, higher rates in later portions of the interval decrease. Rate-dependent effects of morphine on behavior maintained by FI schedules have been reported with rats (e.g., Rhodus, Elsmore, & Manning, 1974), monkeys (e.g., Katz & Goldberg, 1986; McKearney, 1974), and pigeons (e.g., Heifetz & McMillan, 1971; Katz & Goldberg, 1986; Odum et al., 1998).

In the present experiment, choice trials were presented periodically during an FI 1-min schedule (cf. Stubbs et al., 1978). If a relatively short time had elapsed, pecks to one key color produced food. If a relatively long time had elapsed, pecks to the other key color produced food. The effects of morphine on temporal patterning during FIs and accuracy on temporal discrimination trials were examined. The goal was to determine whether changes in directly assessed temporal discrimination would occur in the context of an FI schedule.

METHOD

Subjects

The subjects were 4 adult male White Carneau pigeons (Palmetto Pigeon Plant) with no previous experimental history. Upon arrival at the Psychology Department animal colony, the pigeons had unrestricted access to mixed grain for 2 weeks. Free-feeding weights were calculated as the mean of the last six daily weights and ranged from 564 g to 598 g. The pigeons were maintained at 80% of free-feeding weights through postsession feedings as necessary. When not in experimental sessions, they were individually housed in a temperature-controlled colony under a 12:12 hr light/dark cycle with unrestricted access to water and digestive grit. Sessions were conducted during the light part of the cycle.

Apparatus

Four custom-made experimental chambers, constructed of wood with aluminum front panels, were located in a small darkened room. The internal dimensions of each chamber were 33 cm across the front panel, 31 cm from the front panel to the back wall, and 37.5 cm from the floor to ceiling. Three translucent plastic response keys (2.1 cm diameter) on the front panels were mounted 26 cm from the floor. The keys could be lit from behind with white, green, and red light and required a force of approximately 0.19 N to record a response. A lamp (28 VDC, 1.1 W) 7 cm above the center key served as a houselight. A rectangular aperture 16 cm below the center key provided access to a solenoid-operated food hopper filled with mixed grain. During hopper presentations, the aperture was lit with white light and the houselight and keylights were extinguished. Photocells were mounted on either side of the hopper aperture. Extraneous sounds were masked by white noise and chamber ventilation fans. Contingencies were programmed and data were collected by an MS-DOS-based 80386 microcomputer using the Smart Cumulative Recorder® and an MS-DOS-based 80486 microcomputer programmed under Medstate Notation® (MED Associates, Inc. & Tatham, 1991), located in an adjacent room.

Procedure

Experimental sessions occurred daily at approximately the same time.

Pretraining. The pigeons were first acclimated to the chambers, and were then trained to eat from the food hopper. Based on the pigeons' latency to place their heads in the hopper (i.e., to break the photocell beam inside the hopper aperture), a computer program gradually decreased the hopper duration and increased the time between hopper presentations as the pigeons placed their heads in the hopper more rapidly. Two sessions of hopper training, each terminating following 40 food presentations, were conducted.

Next, key pecks were autoshaped (Brown & Jenkins, 1968). After a varying amount of time averaging 60 s, a key was lit a particular

color for 6 s followed by response-independent presentation of the hopper for 4 s. Pecks to a lit key resulted in immediate hopper access. The center key was lit white and each side key was lit either red or green on any given trial. Key-color and position combinations occurred in random order, each presented eight times per session, for a total of 40 hopper presentations. After two sessions of autoshaping, the pigeons pecked all key-color and position combinations reliably and with short latencies.

Following autoshaping sessions, an FI schedule was in effect on the white center key. The first peck after the interval elapsed turned off the center keylight and houselight and produced 2.5-s access to food, after which the keylight and houselight were lit and the next interval started. Sessions terminated after 40 reinforcer deliveries. In the first session, an FI 5-s schedule was in effect. The FI duration was increased to 15 s and thereafter in 15-s increments across sessions until it reached the terminal duration of 1 min.

An FI duration of 1 min was chosen for several reasons. Programmed session duration was held to approximately 1 hr to minimize potential differences in the time course of the effects of morphine from previous experiments in this laboratory (e.g., Odum et al., 1998; Odum & Schaal, 1999). Furthermore, a sufficient number of choice trials was required to obtain an accurate assessment of temporal discrimination, yet if too many intervals were interrupted by temporal choice trials, characteristic FI patterning could be disrupted by the temporal discrimination procedure.

After three sessions with the final FI duration of 1 min, choice trials were added for a portion of the intervals. During 12 of the 48 total intervals presented during the session, the white center keylight was extinguished after only a part of the interval and the side keys were lit, one green and the other red. The point of subjective equality between two temporal endpoints has been empirically determined to be close to the geometric mean, rather than the arithmetic mean, of the endpoints (e.g., Stubbs, 1968). The shortest and longest temporal choice trial durations used were 2 and 58 s, yielding a geometric mean of 10.77 s. The sample durations on choice trials were spaced in equal logarithmic units around this duration. Choice trials occurred after 2, 4.64, 24.99, and 58 s of the interval had elapsed; each type was presented in random order with the constraint that each appear three times during sessions. For 2 pigeons (P435 and P866), following the shorter durations (2- and 4.64-s trials), a peck to the green key extinguished the keylight and houselight and produced 2.5-s access to food. Following the longer durations (24.99- and 58-s trials), a peck to the red key extinguished the keylight and houselight and produced 2.5-s access to food. Pecks to the incorrect key color produced a 2.5-s blackout. For the 2 remaining pigeons (P582 and P585), the correct colors were reversed (i.e., red was correct following shorter samples, and green was correct following longer samples). During the first session of this procedure, all choices were forced (i.e., only the correct response was presented as an alternative; cf. Stubbs et al., 1978).

Following food or blackout presentation, the center key was lit white and the next interval began. Choice trials were followed by at least one fixed interval not interrupted by a choice trial (cf. Stubbs et al., 1978). Which side key was red and which side key was green during choice trials was randomly determined with the constraint that each color appear on each key an equal number of times during the session. After 14 sessions, accuracy on choice trials remained near chance (50%), choice distributions for all pigeons showed either strong color or position biases, and steps were taken to facilitate acquisition of the temporal discrimination.

The total number of intervals per session was increased to 50 from 48, and the number of those that became temporal choice trials was increased to 20 from 12. Furthermore, only the two most extreme temporal samples (2 and 58 s) were presented, each 10 times per session. After approximately 100 sessions on the two-sample procedure, overall accuracy was high (90% or greater) and stable for all pigeons. The length of, and adjustments in, the required training were similar to that reported by Stubbs et al. (1978) for two sample durations (i.e., "several months, with various modifications," p. 171).

Following acquisition of the temporal discrimination at two durations, the full range

of sample durations (2, 4.64, 24.99, and 58 s) was reintroduced. The pigeons then experienced at least 57 sessions (range, 57 to 97) with the four sample durations prior to morphine administration. A 10-min chamber blackout preceded all sessions. If a programmed reinforcer was not collected within 1 min of when it was scheduled, a 2.5-s blackout occurred and the session continued (i.e., there was a 1-min limited hold in effect for all fixed intervals and choice trials).

Morphine tests. Drug testing began for individual pigeons when overall response rates and indexes of curvature during fixed intervals and choice accuracy on temporal discrimination trials were stable as judged by visual inspection (i.e., they showed no increasing or decreasing trends nor extreme variability over the last 15 to 20 sessions). The index of curvature is a measure of the proportional distribution of responses across fixed intervals (Fry, Kelleher, & Cook, 1960). Fixed intervals were divided into four 15-s bins (the same number used by Stubbs et al., 1978). The number of responses that occurred in each bin was summed across the session for the fixed intervals only (i.e., responses during temporal choice trials were not included). The index of curvature (I) was then calculated for each session using the following formula from Fry et al. (1960):

$$I = 3R_4 - 2(R_1 + R_2 + R_3)/4R_4,$$

where R_1 is the total number of responses occurring in first bin, R_2 is the total number of responses occurring in the first and second bin, R_3 is the total number of responses occurring in the first, second, and third bins, and R_4 is the total number of responses occurring in all of the bins. Calculated in this manner, the possible range of the index is from −.75 (if all responses occurred in the first bin) through 0 (if an equal number of responses occurred in all bins) to +.75 (if all responses occurred in the fourth bin).

Morphine sulfate (obtained from the National Institute on Drug Abuse) was dissolved in 0.9% saline and administered in a volume of 1.0 ml/kg of the body weight at 80% of free feeding. Morphine and vehicle were administered via intramuscular (i.m.) injections into the breast immediately before the pigeons were placed in the experimental chambers. To accustom the pigeons to the injection routine and because initial drug determinations could be influenced by a novelty effect (e.g., Dews, 1962), the pigeons were given four preliminary 3.0 mg/kg doses of morphine. Results from these injections were not included in analyses.

After the preliminary doses, morphine and vehicle were administered in the following order: 3.0 mg/kg, 5.6 mg/kg, 1.0 mg/kg, 10.0 mg/kg, and saline. Tests were separated by at least three consecutive baseline sessions not preceded by an injection. The session that immediately preceded a morphine or vehicle test session was designated a control session. The effects of each dose and the saline vehicle were determined at least three and a maximum of four times. Dose–effect curves were determined completely before any dose was repeated.

RESULTS

Figure 1 shows cumulative records of the performance generated by the FI 1-min schedule with interpolated temporal choice trials for each pigeon. Each record shows performance during the control session prior to the session in which 3.0 mg/kg morphine was administered the second time (i.e., roughly half way through the experiment). In general, pauses occurred after reinforcer deliveries, and high rates of pecking occurred towards the end of intervals. However, for 2 pigeons in particular (P435 and P866), bursts of responses sometimes occurred early in intervals, followed by a pause and a resumption of pecking. These pigeons were often pecking when choice trials were presented after the shorter durations. The median time to the first peck during an interval during control sessions was relatively short for these 2 birds: 3.1 s (P435) and 2.6 s (P866). The other 2 pigeons (P582 and P585) often were not pecking when choice trials were presented after the shorter durations. The median time to the first peck during an interval during control sessions was longer for these 2 birds: 30.3 s (P582) and 20.9 s (P585).

The next two figures display the effects of morphine on pecking during fixed intervals. Center-key pecks that occurred during intervals that become temporal choice trials were not included in these analyses. Figure 2 shows indexes of curvature (Fry et al., 1960) for

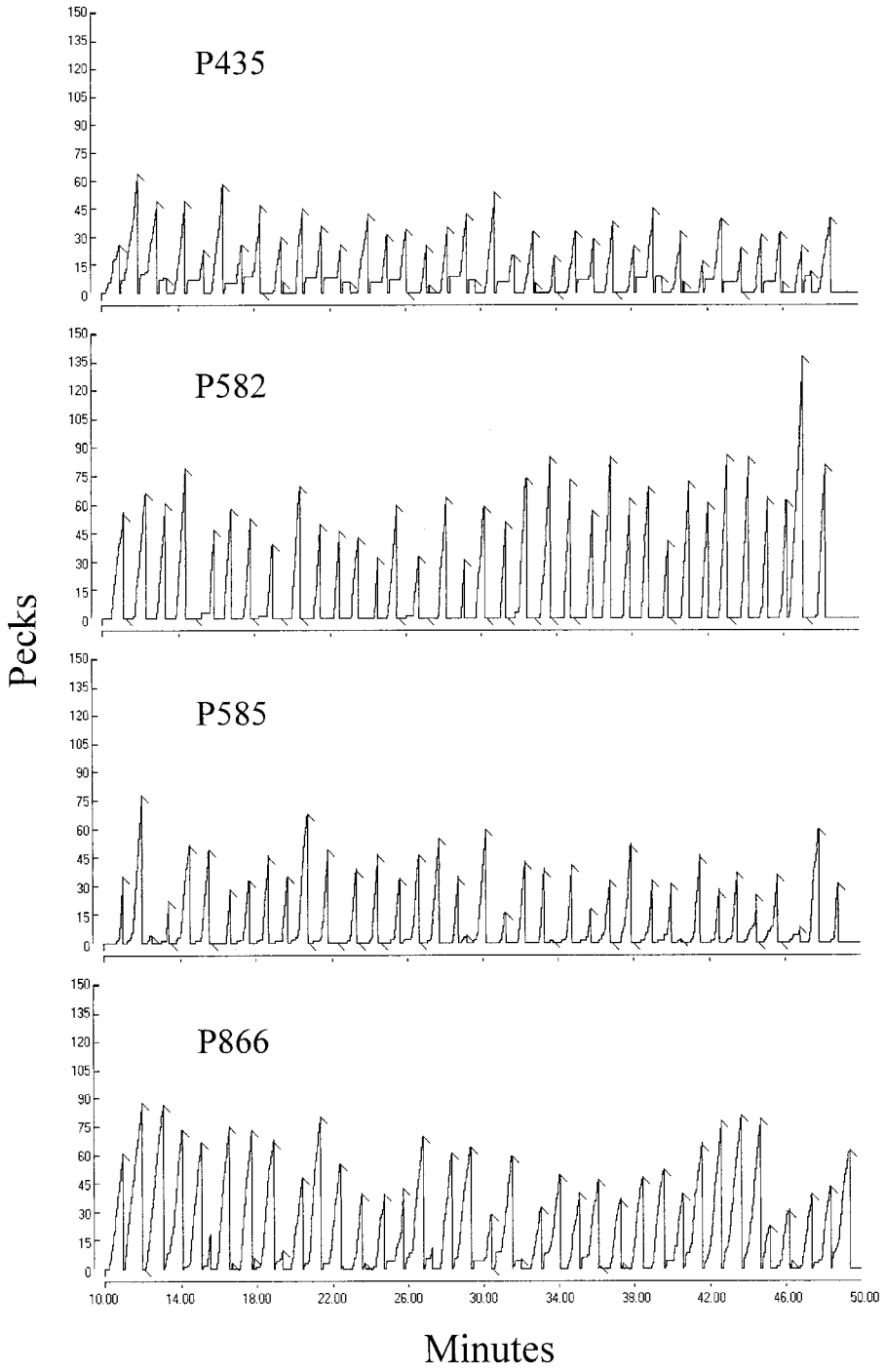

Fig. 1. Sample cumulative records of pecking under control conditions (see text) for each pigeon under the FI 1-min schedule with interpolated temporal choice trials. Diagonal deflections of the pen indicate food presentations (either at the end of fixed intervals or during temporal choice trials). The pen reset to baseline after fixed intervals and temporal choice trials ended. Only pecks to the center key are shown (i.e., pecks to side keys during the choice trials are not included).

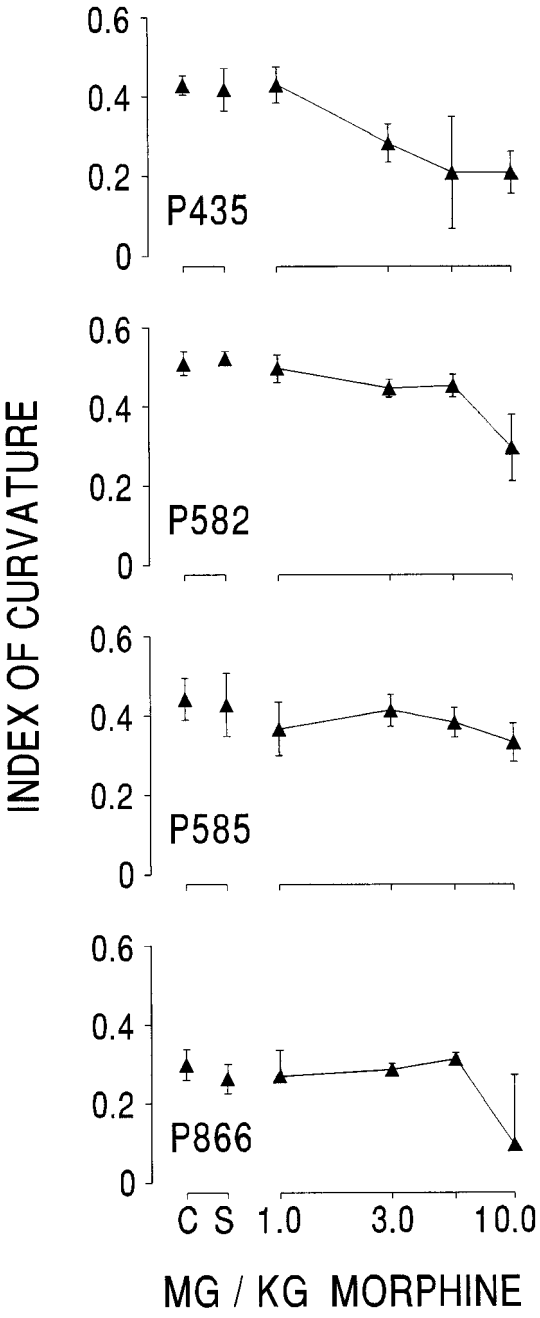

Fig. 2. Effects of injections of morphine on the index of curvature during the FI 1-min portion of the session for each pigeon. Unconnected points show means for all control (C) and saline (S) sessions. Lines connect points showing mean rates for at least three determinations of each dose. Vertical bars represent one standard deviation above and below the mean. Lower bars have been omitted for morphine means for P866. The numbers of sessions contributing to the control means for each pigeon are 16 (P435 and 582), 18 (P585), and 15 (P866).

each pigeon as a function of morphine dose. Control performance shows that indexes of curvature were positive, indicating that relatively more responses occurred later in intervals than earlier in intervals. Indexes were largely unaffected by saline administration. Morphine decreased the index of curvature for all pigeons, particularly at the largest dose. The effects were minimal for P585. The decrease in the index of curvature with morphine administration shows that morphine changed the temporal distribution of responses across the interval so that relatively more responses occurred earlier in the intervals compared to control performance.

Figure 3 shows overall response rates during fixed intervals. The saline vehicle had little effect on overall rates of key pecking. Morphine typically decreased rates of key pecking in a dose-dependent manner. Response rates were largely unaffected at the smallest dose (1.0 mg/kg morphine) and virtually suppressed at the largest dose (10.0 mg/kg morphine). Rates increased for P866 at the smallest dose, however, and rates were not completely suppressed for P585 at the largest dose.

The next two figures display the effects of morphine on accuracy during interpolated temporal choice trials. Figure 4 shows overall accuracy on temporal choice trials as a function of morphine dose for each pigeon. Percentage correct was close to 100% under control conditions and was unaffected by saline administration for each pigeon. The smallest dose of morphine (1.0 mg/kg) had little effect on accuracy. Larger doses, particularly 10.0 mg/kg morphine, decreased accuracy. The effects were comparatively minimal for P435.

To examine more closely the nature of the disruptions in overall accuracy, Figure 5 shows mean percentage of choices corresponding to the long key color as a function of sample duration for each dose of morphine and vehicle for all pigeons. Performance following saline administration was similar to that of control sessions: The percentage of long choices following the two shortest samples was low, and the percentage of long choices following the two longest samples was high. The functions fall at the bisection point of the geometric mean and 50% correct.

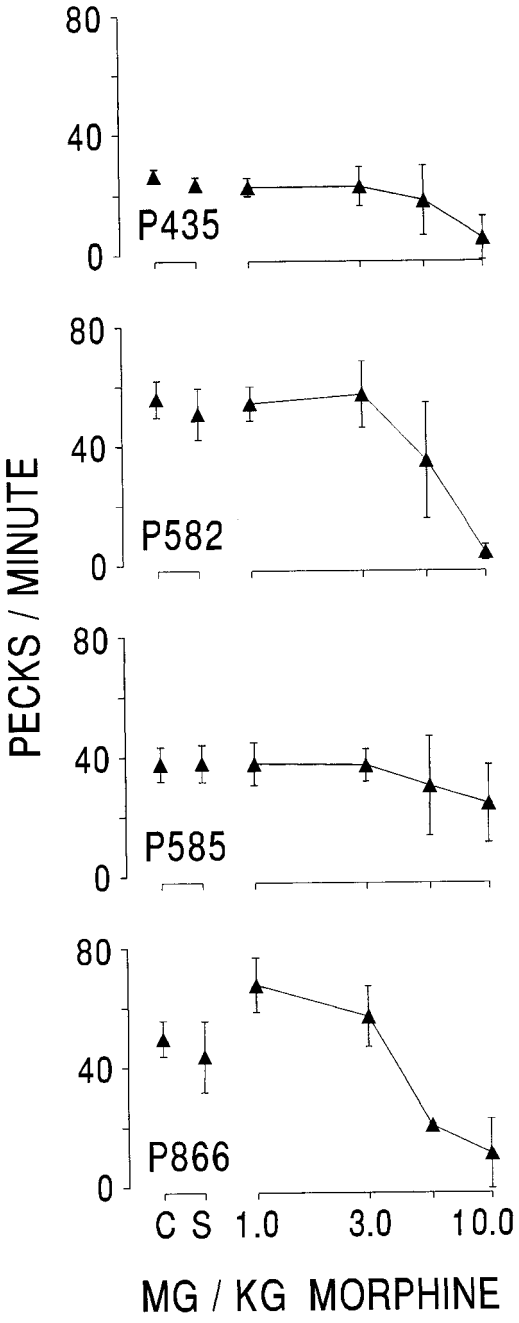

Fig. 3. Effects of injections of morphine on overall rates of key pecking during the FI 1-min portion of the session for each pigeon. Other details as in Figure 2.

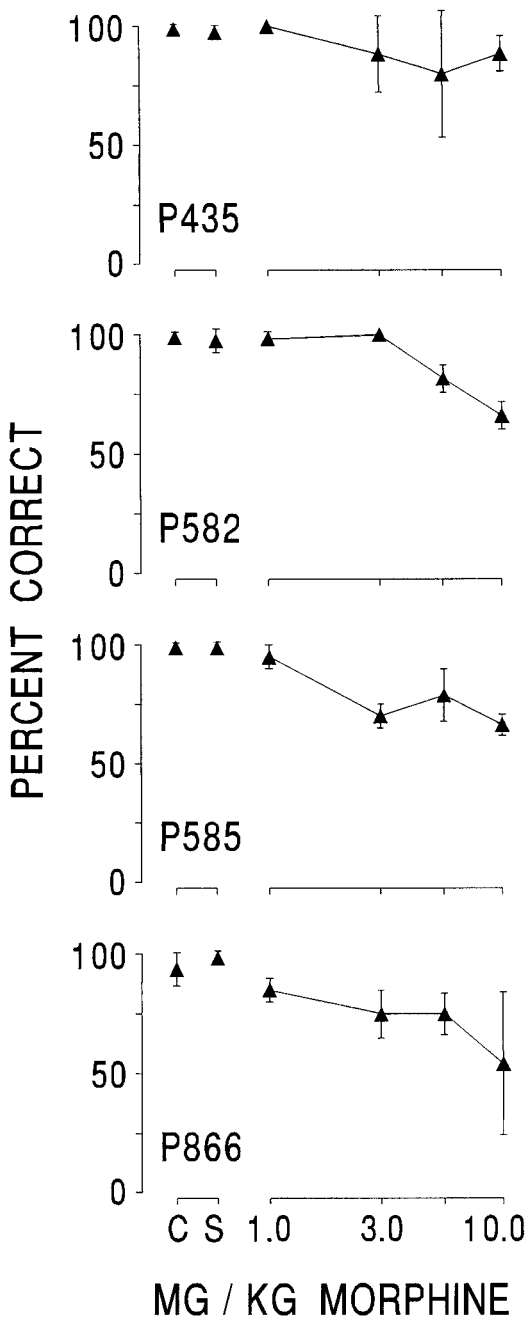

Fig. 4. Effects of injections of morphine on overall accuracy on temporal discrimination trials for each pigeon. Other details as in Figure 2.

The administration of 1.0 mg/kg morphine did not affect accuracy. At 3.0 mg/kg morphine, the functions deviated from control for all pigeons except P582, and at 5.6 mg/kg morphine for all pigeons, with disruptions evident following both long and short sample durations. Although accuracy was disrupted, the functions crossed close to the bisection point for all pigeons, indicative of a

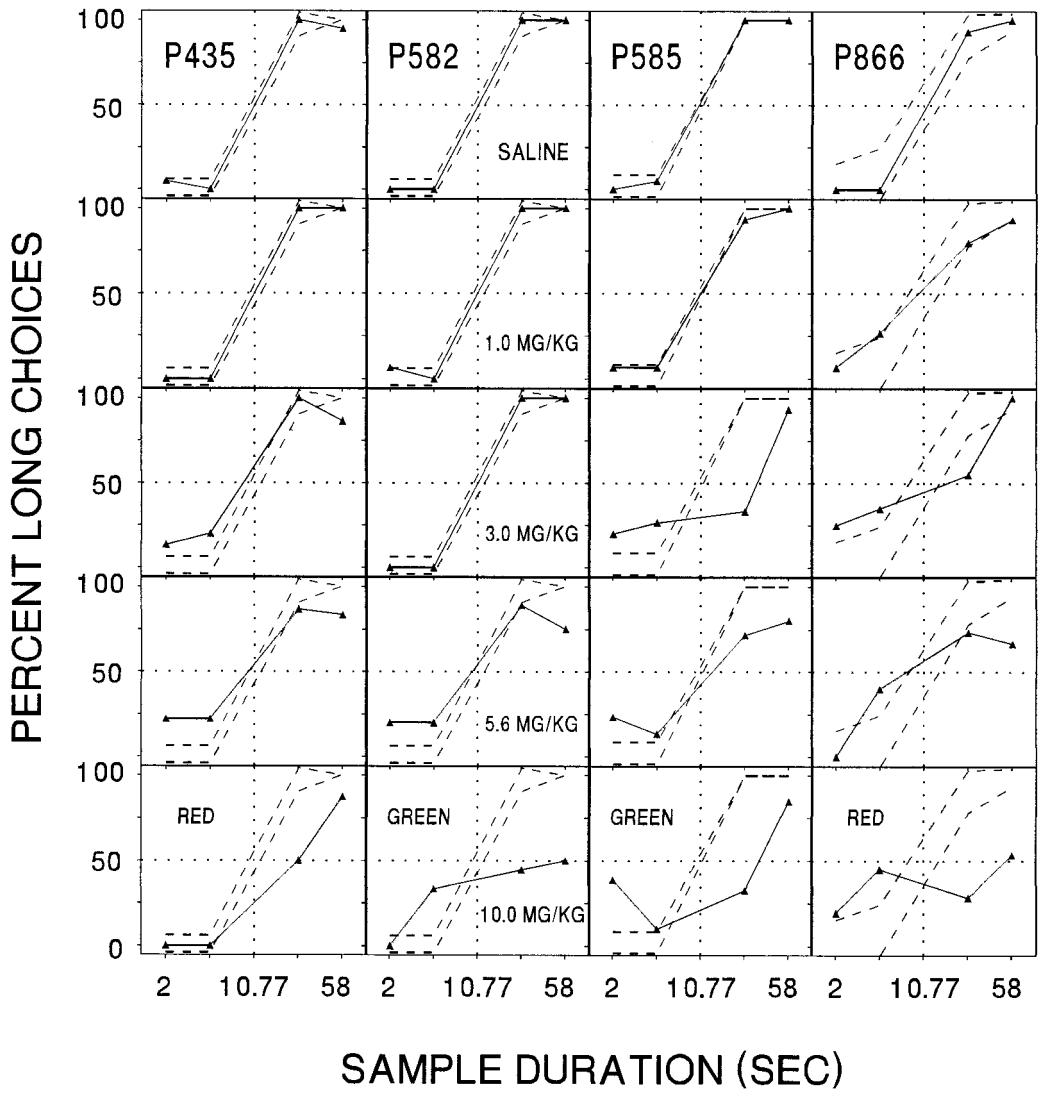

Fig. 5. Percentage of long choices following saline and morphine administration (rows) as a function of sample duration for each pigeon (columns). Note that *x* axis is logarithmic. Solid lines connect points from the means of all determinations of that dose or saline. Dashes indicate one standard deviation above and below control means (control means are not shown). Dots indicate the bisection of 50% accuracy and the geometric mean of the sample duration endpoints. The color that was correct following long samples is indicated in the lower row of panels for each pigeon.

general loss of temporal control over choice responses rather than a specific change toward over- or underestimation. At 10.0 mg/kg morphine, the functions were more variable across pigeons, possibly as a result of the smaller number of choice trials completed (see information below) at this dose. There was still evidence for disruption of accuracy following both long and short sample durations except for P435, for which accuracy was disrupted only following long sample durations. The functions for all pigeons crossed below the bisection point, indicating that accuracy was impaired somewhat more following long sample durations at this dose.

There were no systematic differences in the functions obtained for pigeons for which red was correct following long sample durations (P435 and P866) compared to those obtained for pigeons for which green was correct fol-

lowing long sample durations (P582 and P585). Also, there were no obvious differences for pigeons that commonly were pecking when choice trials were presented after shorter durations (P435 and P866) and pigeons that commonly were not pecking when choice trials were presented after shorter durations (P582 and P585; see cumulative records in Figure 1).

Two important considerations about the effects of morphine on temporal choice trial accuracy concern the latency for the pigeons to make a choice and the number of trials on which they made no choice (i.e., on which the 1-min limited hold elapsed). Table 1 shows latencies to make choice responses for each pigeon during control, saline, and morphine sessions as a function of whether or not the choice was correct. Trials on which a pigeon did not make a choice response are not included (see below). Under control conditions, choice responses on average usually occurred within 1 or 2 s of when the choice trials were presented. There were no systematic differences in latencies between correct and incorrect choices. There were also no obvious differences for choice latencies made following shorter or longer temporal samples (data not shown). Morphine tended to increase the mean latency and standard deviation for both correct and incorrect choices (most clearly for P582 after 5.6 mg/kg morphine and for P866 after 10.0 mg/kg morphine), although there were no obvious changes in mean latencies for P585. In summary, across pigeons and conditions, if a choice was made on a choice trial, it usually occurred relatively soon after the trial was presented.

The total number of choice trials completed was affected by larger doses of morphine. At larger doses, morphine decreased the total number of choice trials completed due to the lapse of the 1-min limited hold for choices. Under control conditions and following saline administration, the pigeons completed all possible choice trials. No limited holds elapsed for any pigeon after 1.0 mg/kg or 3.0 mg/kg morphine either. However, following administration of 5.6 mg/kg morphine, out of 20 possible choice trials, pigeons completed on average 16.2 (P435), 18.7 (P582), 18 (P585), and 20 (P866) trials. Following administration of 10.0 mg/kg morphine, the total number of trials completed on average was 7.3 (P435), 7.7 (P582), 18.5 (P585), and 17.3 (P866). Thus, morphine decreased the number of temporal choice trials on which pigeons made a choice. There were no differences between the number of trials completed following shorter or longer temporal samples under any conditions (data not shown).

DISCUSSION

In general, results were consistent with those of previous related experiments. Morphine produced dose-dependent decreases in overall response rates and changed the temporal distribution of responses during fixed intervals as measured by the index of curvature (e.g., Odum & Schaal, 1999; Rhodus et al., 1974). In the direct assessment of the effects of morphine on temporal discrimination, the present results confirm the decreases in accuracy produced by morphine found by Wenger at al. (1995).

In general, morphine decreased overall accuracy on temporal choice trials at doses that tended to decrease overall response rates. This effect is similar to that reported by Wenger et al. (1995) in a direct assessment of the effects of morphine on temporal discrimination in a discrete-trial procedure with pigeons. Wenger et al. found a statistically significant decrease in accuracy only at the dose of morphine that also produced a statistically significant decrease in response rates. In the present experiment there was not necessarily a one-to-one correspondence between the measures for individual pigeons. For example, for P866, accuracy decreased slightly after administration of 1.0 mg/kg morphine, but overall response rates increased. Also, for P866 and P585, accuracy decreased after 3.0 mg/kg morphine, but overall response rates were relatively unaffected. It is noteworthy, however, that the relation between decreases in rates and decreases in accuracy of temporal discrimination following morphine administration was, in general, similar when choice trials were presented alone (Wenger et al., 1995) or imbedded in the context of an FI schedule (the present experiment).

There are several alternative explanations to the possibility that morphine decreased accuracy on choice trials by changing temporal

Table 1

Mean choice latency in seconds and standard deviation (in parentheses) for control sessions (see text) and sessions following morphine or vehicle (saline) administration for possible choice outcomes (correct or incorrect) for each pigeon. One dash indicates that incorrect choices occurred during only one session contributing to the mean. Two dashes indicate that no incorrect choices occurred during any sessions contributing to the mean.

Subject	Choice outcome	Control	Saline	Morphine dose			
				1.0 mg/kg	3.0 mg/kg	5.6 mg/kg	10.0 mg/kg
P435	Correct	2.13 (1.01)	2.22 (0.88)	2.45 (0.97)	2.33 (0.91)	2.67 (1.31)	3.55 (1.27)
	Incorrect	1.95 (1.84)	1.25 (0.21)	— (—)	1.40 (0.52)	2.55 (2.05)	1.95 (0.50)
P582	Correct	1.15 (0.19)	1.21 (0.14)	1.01 (0.36)	1.39 (0.27)	4.26 (4.91)	1.82 (0.62)
	Incorrect	1.60 (0.78)	1.85 (—)	2.1 (—)	— (—)	6.13 (6.35)	2.41 (0.61)
P585	Correct	1.65 (0.32)	1.58 (0.31)	1.51 (0.29)	1.27 (0.06)	2.03 (1.32)	1.60 (0.34)
	Incorrect	1.83 (0.91)	2.4 (—)	2.3 (0.42)	1.62 (0.40)	1.84 (0.28)	1.88 (0.77)
P866	Correct	1.56 (0.14)	1.42 (0.11)	1.26 (0.13)	1.39 (0.13)	2.86 (1.52)	4.47 (4.42)
	Incorrect	2.01 (1.35)	1.5 (—)	1.67 (0.22)	1.43 (0.15)	2.04 (0.30)	6.92 (4.80)

discrimination. One unlikely explanation for the present results is that morphine decreased accuracy by producing a color bias rather than by changing temporal discrimination. As seen in Figure 5, morphine changed accuracy in a similar manner for birds for which red was correct following long samples and for which green was correct following long samples.

Similarly, increases in latencies to make a choice and decreases in the number of choice trials completed do not seem to totally account for the present results either. Although latencies to make a choice indeed increased somewhat for some birds at particular doses of morphine, the changes do not seem to be large or consistent enough to solely account for the changes in accuracy on choice trials. At larger doses, morphine decreased the number of trials on which the pigeons made a choice. Changes in accuracy were apparent at doses at which the pigeons completed all of the choice trials, however, which rules out the possibility that changes in accuracy were solely a function of the decreased number of choice trials completed.

Another alternative explanation for the present results is that morphine may have disrupted stimulus control independently of its effects on temporal discrimination. In other words, morphine may have changed accuracy on choice trials by producing a generalized decrement in conditional discriminative control without changing temporal discrimination per se. However, several experiments with pigeons have found no effect of morphine doses as large as 10.0 mg/kg on accuracy in delayed matching-to-sample procedures with red and green samples (McMillan, 1981; Picker, Massie, & Dykstra, 1987; Wenger, Hudzik, & Wright, 1993). Thus, although the results of the present experiment cannot rule out the possibility that morphine changed accuracy on choice trials by changing stimulus control independently of any changes in temporal discrimination, the results of previous experiments render this explanation less compelling.

Despite the number of alternative explanations for the present results that may be ruled out, this experiment does have several limitations. First, the steps taken to minimize the possibility that the interpolated temporal choice trials would disrupt the temporal patterning of responses during fixed intervals were not entirely successful. As seen in Figure 1, for at least 2 pigeons relatively high response rates occurred early in the fixed intervals around the time that choice trials following short sample durations were presented independently of responding. This effect is similar to that reported by Lattal and Bryan (1976, Experiment 3) for pigeons when response-independent reinforcers were presented at regular times during fixed intervals. Whether the early responding during fixed intervals contributed in some way to the present results is not clear. The effects of morphine on temporal patterning during fixed intervals and on choice accuracy, however, did not appear to be different for birds that did not show these early higher response

rates during fixed intervals under control conditions.

Another limitation of the present experiment is that the measures of accuracy on temporal choice trials and the measure of temporal patterning during fixed intervals could have been more sensitive. For example, there were only four durations of temporal samples, and they were relatively widely spaced. The limited number of samples was used to provide enough presentations of each sample duration (five per session) to obtain reliable measures of accuracy at each sample duration. The total number of choice trial presentations per session was limited to 20 in an attempt (not entirely successful) to minimize potential changes in FI patterning. The limited number of sample durations, however, may have produced a measure of temporal discrimination that was less sensitive than what would have been obtained if more sample durations had been presented. Similarly, future experiments would benefit from a more sensitive measure of temporal patterning during fixed intervals. The interval could be divided more finely for the calculation of the index of curvature and other measures of temporal patterning (e.g., the times at which responding started in the interval and the variance in those times) could be included as well. Finer grained measures could allow an examination of the relation between the temporal patterning of responses during the interval and accuracy on temporal choice trials.

In spite of these limitations, the present experiment did achieve the goal of determining whether morphine produced changes in directly assessed temporal discrimination in the context of an FI schedule. Morphine changed not only the temporal patterning of responses during the interval but also decreased the probability of correctly choosing a key color given a particular sample duration. Changes in the accuracy of the temporal discrimination were not confined to short or long sample durations. The flattening of the temporal generalization gradient is consistent with interpretations of patterning changes during FI schedules as accompanied by general changes in temporal discrimination. These results do not support, however, interpretations of rate increases early in fixed intervals as an overestimation of elapsed time (e.g., McAuley & Leslie, 1986), or as due to an increase in the speed of a hypothesized internal clock (e.g., Maricq et al., 1981; Meck, 1996). Overestimation of time (resulting from an increase in clock speed or otherwise) would shift temporal generalization gradients to the left (i.e., selectively disrupt accuracy following short sample durations) and not flatten those gradients (i.e., disrupt accuracy following both long and short sample durations). Whether the present results would be replicated with a larger number of sample durations remains to be seen.

The results of the present experiment cannot determine whether changes in temporal discrimination produced changes in response patterning, whether changes in response patterning produced changes in temporal discrimination, or whether changes in a third factor produced changes in temporal discrimination and response patterning. Positively accelerated response rates during fixed intervals, however, were evident within the first few sessions of training. Following these first few sessions containing only fixed intervals, the temporal discrimination trials were introduced. After 14 additional sessions, accuracy was still at chance (50%) and the procedure was modified to facilitate the development of the discrimination. Accuracy did not reach high stable levels until after many sessions. Thus, consistent with Stubbs et al. (1978), accuracy on temporal discrimination trials took longer to develop than temporal patterning. Therefore, it seems unlikely that temporal discrimination produced response patterning, as the latter developed before the former, and it is possible that performance on temporal discrimination trials was in some way based on response patterning. This suggestion is consistent at a heuristic level with the behavioral theory of timing (Killeen & Fetterman, 1988), which maintains that behavior occurring regularly in time may come to serve as the basis for discriminations of the passage of time.

The disruptions in the temporal patterning of responses and accuracy on temporal discrimination trials produced in the present experiment were similar to the effects produced by Stubbs et al. (1978) with a nonpharmacological disrupter. Stubbs and colleagues decreased indexes of curvature and accuracy by occasionally substituting brief stimuli for food as the consequent event at the end of fixed

intervals, whereas in the present experiment indexes of curvature and accuracy were decreased by morphine administration. The analogous results raise the possibility that morphine may change accuracy and patterning in a manner that is not specific to its action as a pharmacological agent.

In fact, the rate-dependent changes in FI patterning reported in the literature of behavioral pharmacology resemble disruptions in FI patterning produced by the introduction of ''extra stimuli'' during fixed intervals (see Howell, Byrd, & Marr, 1986; McKim, 1981). For example, when Hinrichs (1968) maintained the key pecking of pigeons on an FI schedule of food delivery, changing the color of the response key for selected intervals increased rates of key pecking early during intervals and decreased rates late in the intervals compared to performance during intervals with the original color. When the test color was presented during all intervals for many sessions, typical FI response patterning returned. When the original color was then presented during selected intervals (as the test color had been previously), rates early in the interval increased, and rates later in the interval decreased, compared to performance during what had previously been the test color. The results are not strictly attributable to the novelty of the test stimulus, because the pigeons had extensive experience with the original key color when it was reintroduced. Rather, this effect has been attributed to the change in stimulus conditions per se (see Howell et al., 1986; McKim, 1981). Analogous effects have been produced with humans by presenting or removing white noise (Azrin, 1958, Experiment 1), with a pigeon by changing the key color and FI duration simultaneously (Ferster & Skinner, 1957, pp. 319–320), with rats by presenting a tone and by vibrating the chamber (Flanagan & Webb, 1964), and with rats by presenting a buzzer (Singh & Wickens, 1968).

Noting the apparent similarity to the effects of drugs on FI schedule performance, McKim (1981) suggested that rate dependency following drug administration was related to the effects observed on FI performance following the presentation of extra stimuli. Specifically, he proposed that, to the extent that the stimulus properties of drugs are similar to the properties of conventional environmental stimuli, drug-produced stimuli and conventional stimuli will disrupt behavior in a similar manner. Howell et al. (1986) tested this proposition by comparing the effects of a range of intensities of white noise presentation and a range of doses of cocaine on the FI performance of monkeys. Both manipulations produced similar and durable results: Low rates during the beginning of the interval increased, and high rates later in the interval decreased. McKim (1973) reported analogous effects on the FI performance of rats with white noise presentation and scopolamine administration. These types of results suggest that drugs and more conventional stimuli may change FI patterning through a similar mechanism.

In summary, the present experiment provided evidence that morphine changed both the temporal patterning of responses during an FI schedule and the accuracy of responses during interpolated temporal discrimination trials in the context of an FI schedule. Thus, changes in discriminative control by time are supported as a possible behavioral mechanism of the effects of morphine on performance under FI schedules. The present experiment did not find any evidence, however, to support the view that changes produced by drugs in temporal patterning under FI schedules represent selective overestimation of elapsed time. Future experiments should attempt to establish more precisely the relation between changes in response patterning and temporal choice trial accuracy.

REFERENCES

Azrin, N. H. (1958). Some effects of noise on human behavior. *Journal of the Experimental Analysis of Behavior, 1,* 183–200.

Branch, M. N. (1984). Rate dependency, behavioral mechanisms, and behavioral pharmacology. *Journal of the Experimental Analysis of Behavior, 42,* 511–522.

Branch, M. N., & Gollub, L. R. (1974). A detailed analysis of the effects of *d*-amphetamine on behavior under fixed-interval schedules. *Journal of the Experimental Analysis of Behavior, 21,* 519–539.

Brown, P. L., & Jenkins, H. M. (1968). Autoshaping of the pigeon's key-peck. *Journal of the Experimental Analysis of Behavior, 11,* 1–8.

Catania, A. C. (1970). Reinforcement schedules and psychophysical judgments: A study of some temporal properties of behavior. In W. N. Schoenfeld (Ed.), *Theory of reinforcement schedules* (pp. 1–42). New York: Appleton-Century-Crofts.

Church, R. M. (1997). Timing and temporal search. In

C. M. Bradshaw & E. Szabadi (Eds.), *Time and behaviour* (pp. 41–78). Amsterdam: Elsevier.

Dews, P. B. (1962). Psychopharmacology. In A. J. Bachrach (Ed.), *Experimental foundations of clinical psychology* (pp. 423–441). New York: Basic Books.

Dews, P. B. (1981). History and present status of rate-dependency investigations. In T. Thompson, P. B. Dews, & J. E. Barrett (Eds.), *Advances in behavioral pharmacology* (Vol. 3, pp. 111–118). New York: Academic Press.

Dews, P. B., & Wenger, G. R. (1977). Rate-dependency of the behavioral effects of amphetamine. In T. Thompson & P. B. Dews (Eds.), *Advances in behavioral pharmacology* (Vol. 1, pp. 167–227). New York: Academic Press.

Ferster, C. B., & Skinner, B. F. (1957). *Schedules of reinforcement.* New York: Appleton-Century-Crofts.

Flanagan, B., & Webb, W. B. (1964). Disinhibition and external inhibition in fixed interval operant conditioning. *Psychonomic Science, 1,* 123–124.

Fry, W., Kelleher, R. T., & Cook, L. (1960). A mathematical index of performance on fixed-interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior, 3,* 193–199.

Gentry, G. D., Weiss, B., & Laties, V. G. (1983). The microanalysis of fixed-interval responding. *Journal of the Experimental Analysis of Behavior, 39,* 327–343.

Heifetz, S. A., & McMillan, D. E. (1971). Development of behavioral tolerance to morphine and methadone using the schedule-controlled behavior of the pigeon. *Psychopharmacologia, 19,* 40–52.

Higa, J. J., & Staddon, J. E. R. (1997). Dynamic models of rapid temporal control in animals. In C. M. Bradshaw & E. Szabadi (Eds.), *Time and behaviour* (pp. 1–40). Amsterdam: Elsevier.

Hinrichs, J. V. (1968). Disinhibition of delay in fixed-interval instrumental conditioning. *Psychonomic Science, 12,* 313–314.

Howell, L. L., Byrd, L. D., & Marr, M. J. (1986). Similarities in the rate-altering effects of white noise and cocaine. *Journal of the Experimental Analysis of Behavior, 46,* 381–394.

Katz, J. L., & Goldberg, S. R. (1986). Effects of ethylketazocine and morphine on schedule-controlled behavior in pigeons and squirrel monkeys. *Journal of Pharmacology and Experimental Therapeutics, 239,* 433–441.

Kelleher, R. T., & Morse, W. H. (1968). Determinants of the specificity of the behavioral effects of drugs. *Ergebnisse der Physiologie Biologischen Chemie und Experimentallen Pharmakologie, 60,* 1–56.

Keller, F. S., & Schoenfeld, W. N. (1950). *Principles of psychology.* New York: Appleton-Century-Crofts.

Killeen, P. R. (1991). Behavior's time. In G. H. Bower (Ed.), *The psychology of learning and motivation* (pp. 295–334). New York: Academic Press.

Killeen, P. R., & Fetterman, J. G. (1988). A behavioral theory of timing. *Psychological Review, 95,* 274–295.

Killeen, P. R., Fetterman, J. G., & Bizo, L. A. (1997). Time's causes. In C. M. Bradshaw & E. Szabadi (Eds.), *Time and behaviour* (pp. 79–132). Amsterdam: Elsevier.

Lattal, K. A., & Bryan, A. J. (1976). Effects of concurrent response-independent reinforcement on fixed-interval schedule performance. *Journal of the Experimental Analysis of Behavior, 26,* 495–504.

Maricq, A. V., Roberts, S., & Church, R. M. (1981). Methamphetamine and time estimation. *Journal of Experimental Psychology: Animal Behavior Processes, 7,* 18–30.

McAuley, F., & Leslie, J. C. (1986). Molecular analyses of the effects of *d*-amphetamine on fixed-interval schedule performance of rats. *Journal of the Experimental Analysis of Behavior, 45,* 207–219.

McKearney, J. W. (1974). Effects of *d*-amphetamine, morphine, and chlorpromazine on responding under fixed-interval schedules of food presentation or electric shock presentation. *Journal of Pharmacology and Experimental Therapeutics, 190,* 141–153.

McKearney, J. W. (1981). Rate dependency: Scope and limitations in the explanation and analysis of the behavioral effects of drugs. In T. Thompson, P. B. Dews, & J. E. Barrett (Eds.), *Advances in behavioral pharmacology* (Vol. 3, pp. 91–109). New York: Academic Press.

McKearney, J. W., & Barrett, J. E. (1978). Schedule-controlled behavior and the effects of drugs. In D. E. Blackman & D. J. Sanger (Eds.), *Contemporary research in behavioral pharmacology* (pp. 1–68). New York: Plenum Press.

McKim, W. A. (1973). The effects of scopolamine on fixed-interval behavior in the rat: A rate-dependency effect. *Psychopharmacologia, 32,* 255–264.

McKim, W. A. (1981). Rate-dependency: A nonspecific behavioral effect of drugs. In T. Thompson, P. B. Dews, & J. E. Barrett (Eds.), *Advances in behavioral pharmacology* (Vol. 3, pp. 61–73). New York: Academic Press.

McMillan, D. E. (1981). Effects of chemicals on delayed matching behavior in pigeons I: Acute effects of drugs. *Neurotoxicology, 2,* 485–498.

Meck, W. H. (1996). Neuropharmacology of timing and time perception. *Cognitive Brain Research, 3,* 227–242.

MED Associates, Inc., & Tatham, T. A. (1991). *MED-PC Medstate notation.* East Fairfield, NH: MED Associates, Inc.

Odum, A. L., Haworth, S. C., & Schaal, D. W. (1998). Food-deprivation level alters the effects of morphine on pigeons' key pecking. *Journal of the Experimental Analysis of Behavior, 69,* 295–310.

Odum, A. L., & Schaal, D. W. (1999). The effects of morphine on clocked fixed-interval performance: Stimulus function or strength of stimulus control? *Behavioural Pharmacology, 10,* 243–255.

Picker, M., Massie, C. A., & Dykstra, L. A. (1987). Evaluation of the effects of opioid agonists and antagonists under a delayed matching-to-sample procedure in pigeons. *Psychopharmacology, 93,* 230–236.

Reynolds, G. S. (1975). *A primer of operant conditioning.* Glenview, IL: Scott Foresman.

Rhodus, D. M., Elsmore, T. F., & Manning, F. J. (1974). Morphine and heroin effects on multiple fixed-interval schedule performance in rats. *Psychopharmacologia, 40,* 147–155.

Roberts, W. A. (1997). Does a common mechanism account for timing and counting phenomena in the pigeon? In C. M. Bradshaw & E. Szabadi (Eds.), *Time and behaviour* (pp. 185–216). Amsterdam: Elsevier.

Sanger, D. J. (1987). Effects of drugs on schedule-controlled behavior. In A. J. Greenshaw & C. T. Dourish (Eds.), *Experimental psychopharmacology* (pp. 213–261). Clinton, NJ: Humana Press.

Sanger, D. J., & Blackman, D. E. (1976). Rate-dependent

effects of drugs: Review of the literature. *Pharmacology Biochemistry and Behavior, 4,* 73–83.

Singh, D., & Wickens, D. D. (1968). Disinhibition in instrumental conditioning. *Journal of Comparative and Physiological Psychology, 66,* 557–559.

Stubbs, D. A. (1968). The discrimination of stimulus duration by pigeons. *Journal of the Experimental Analysis of Behavior, 11,* 223–238.

Stubbs, D. A., Vautin, S. J., Reid, H. M., & Delehanty, D. L. (1978). Discriminative functions of schedule stimuli and memory: A combination of schedule and choice procedures. *Journal of the Experimental Analysis of Behavior, 29,* 167–180.

Wenger, G. R., Hudzik, T. J., & Wright, D. W. (1993). Titrating matching-to-sample performance in pigeons: Effects of diazepam, morphine, and cholinergic agents. *Pharmacology Biochemistry and Behavior, 46,* 435–443.

Wenger, G. R., McMillan, D. E., Moore, E., & Williamson, A. P. (1995). Disruption of temporal discrimination by drugs of abuse: I. Unmasking of a color bias. *Behavioural Pharmacology, 6,* 297–310.

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